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ANINDOBOTHRIUM N. GEN. (EUCESTODA: TETRAPHYLLIDEA) INHABITING MARINE AND FRESHWATER POTAMOTRYGONID STINGRAYS

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ABSTRACT: *Anindobothrium* n. gen. is proposed to accommodate *Caulobothrium anacolum* inhabiting *Himantura schmardae* from Colombia, and 2 new species, one inhabiting *Potamotrygon orbigny* in Brazil and the other inhabiting *Paratrygon aereiba* in Venezuela. Members of the new genus resemble members of *Pararhinebothroides*, *Rhinebothroides*, and *Anthocephalum* by having bothridia with poorly differentiated apical suckers and vasa deferentia expanded into external seminal vesicles. It further resembles *Pararhinebothroides*, *Rhinebothroides*, and *Anthocephalum cairae* by having vas deferens inserted near the poral rather than aporal end of the cirrus sac. The 3 species assigned to the new genus form an apparent monophyletic group, based on the possession of 3 putative synapomorphies: (1) genital pores in the anterior ¼ of the proglottid, a trait that is unusual, but not unique, among phyllobothriids; (2) anteroventral ovarian lobes converging to the center of the proglottid, a character not previously reported for phyllobothriids; and (3) ovarian lobes comprising a loose network of digitiform processes.

Most species of stingrays are marine, although some occasionally enter freshwater systems. Neotropical stingrays (*Paratrygon* Duméril, 1865; *Plesiотrygon* Rosa, Castello, and Thorson, 1987; and *Potamotrygon* Garman, 1913) are obligatory freshwater inhabitants exhibiting low tolerance to saline waters (Thorson, 1970; Thorson et al., 1978; Nishida, 1990). The phylogenetic affinity of this group of elasmobranchs with marine stingrays has generated debate. Brooks, Thorson, and Mayes (1981) noted that the parasites of potamotrygonids known at that time were most closely related to parasites inhabiting members of the marine genus *Urobatis* Garman, 1913. Subsequent studies have suggested that the helminth fauna of potamotrygonids has a complex origin, with various groups showing affinities to parasites inhabiting members of *Urobatis*, *Dasyatis* Rafinesque, 1810, *Himantura* Müller and Henle, 1837, and even sharks (Brooks, 1992, 1995; Brooks and Deardorff, 1988; Hoberg et al., 1998; Marques et al., 1995, 1996, 1997; Monks et al., 1996; Zamparo et al., 1999; Marques, 2000).

Lovejoy (1996, 1997) and McEachran et al. (1996) suggested that the amphi-American clade of *Himantura schmardae* (Werner, 1904) + *Himantura pacifica* (Beebe and Tee-Van, 1941) is the sister group of potamotrygonids, with *Taeniura* Müller and Henle, 1837 being the sister group of that clade. McEachran et al. (1996) included *Taeniura* and the amphi-American *Himantura* within Potamotrygonidae. Based on a total evidence study of 4 mitochondrial genes and 65 morphological characters, Marques (2000) suggested that whereas support for the clade of amphi-American *Himantura* + potamotrygonids was strong, the placement of *Taeniura* was ambiguous; consequently, his conception of the Potamotrygonidae includes the amphi-American *Himantura* and the neotropical freshwater rays.

To date, members of 2 genera of phyllobothriid cestodes have been reported in freshwater potamotrygonids: *Rhinebothroides* Mayes, Brooks, and Thorson, 1981 with 7 nominal species inhabiting exclusively freshwater potamotrygonids, and *Rhinebothrium* Linton, 1889, a genus comprised of species inhabiting

marine elasmobranchs, of which only a single species is known from freshwater potamotrygonids.

Brooks (1977) described *Rhinebothrium magniphallum*, *Rhinebothrium tetralobatum*, and *Caulobothrium anacolum* from *H. schmardae* from the Caribbean Sea, and Marques et al. (1996) described *Rhinebothrium geminum* in *H. pacifica* from the Pacific coast of Costa Rica. *Rhinebothrium magniphallum* and *R. geminum* appear to be closely related to each other, based on their shared possession of a distinctively large cirrus sac, presumably a synapomorphy, and similarities in other diagnostic features (bothridial loculi form, number of bothridial loculi, and number of testes). *Rhinebothrium tetralobatum* is a member of a clade that includes *Rhinebothrium paratrygoni* Rêgo and Dias, 1979 inhabiting freshwater potamotrygonids, but it is not its sister species (see Brooks and Deardorff, 1988).

Caulobothrium anacolum has been an enigmatic species. Brooks (1977) assigned the species to *Caulobothrium* Baer, 1948, because it exhibited bothridia with transverse septa and no marginal loculi or apical suckers and possessed postvaginal testes, but they also noted a number of characters exhibited by the new species that were not reported in other members of the genus. The most recent diagnosis of the genus (Euzet, 1994) fails to include most species assigned to *Caulobothrium*, which appear to represent at least 2 different lineages, one characterized by bothridia having transverse septa only, compact ovaries, and a relatively small number of testes, including some that are postovarian; the other lineage is characterized by bothridia with transverse septa and a medial longitudinal septum, digitiform ovaries, and a relatively large number of testes, none of which is postovarian (Brooks, Mayes, and Thorson, 1981).

No putative close relative of *Rhinebothroides* is known to inhabit *H. schmardae*, *H. pacifica*, or *Taeniura* spp. The most recent phylogenetic analysis of *Rhinebothroides* and relatives suggests that the genus is the sister group of *Pararhinebothroides hobergi* Zamparo, Brooks, and Barriga, 1999, based on their shared possession of the vas deferens inserting into the cirrus sac near the poral end, rather than at the aporal end, a feature unique among tetracophyllideans (Zamparo et al., 1999). *Pararhinebothroides hobergi* inhabits *Urobatis tumescentis* McEachran and Chirichigno in southern Ecuador. The sister group of *Pararhinebothroides* + *Rhinebothroides* is the paraphyletic *Anthocephalum* Linton, 1890 that includes species inhabiting stingrays of various genera (Ruhnke, 1994).

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TABLE I. List of the hosts examined from the Museo de Historia Natural La Salle (MHNLS), Caracas, Venezuela.

Species	Locality (material collected)
<i>Paratrygon aierei-ba</i>	Caño Guaritico, Hato el Frío, Orinoco Basin, Apure, Venezuela (4 specimens [MHNLS 6194, 6197, 6205, 6206]).
<i>Potamotrygon orbignyi</i>	Caño Guaritico, Hato el Frío, Orinoco Basin, Apure, Venezuela (1 specimen [MHNLS 6188]); Caño Macanilla, Hato el Frío, Orinoco Basin, Apure, Venezuela (2 specimens [MHNLS 6001, 6199]); Caño Magaletal, Hato La Ballera, Orinoco Basin, Apure, Venezuela (1 specimen [MHNLS 6208]).
<i>Potamotrygon</i> sp.	Caño Guaritico, Hato el Frío, Orinoco Basin, Apure, Venezuela (15 specimens [MHNLS 6187, 6189–6193, 6191, 6192, 6198, 6200–6204, 6209]); Caño Magaletal, Hato La Ballera, Orinoco Basin, Apure, Venezuela (1 specimen [MHNLS 6209]).

The present study describes 2 new species of phyllobothriids inhabiting potamotrygonids, all of which exhibit external seminal vesicle insertions near the poral end of the cirrus sac. Re-examination of *C. anacolum* revealed that it also exhibits this trait. To accommodate these findings taxonomically, we propose a new genus to receive *C. anacolum* and 2 new species of phyllobothriids inhabiting freshwater potamotrygonids.

MATERIALS AND METHODS

Freshwater potamotrygonids were collected using long-lines from the Amazon and northeastern Brazil during September–December 1996 (see Marques [2000] for the list of hosts and localities). Cestodes were removed from the spiral valve, placed in freshwater, and fixed with hot alcohol–formalin–acetic acid for 24 hr prior to transfer to 70% ethanol for storage. The spiral valve was fixed in warm solution of 10% formalin for later examination. Additional cestodes were obtained from hosts collected in the Orinoco drainage in Venezuela, during October 1991 and August 1997 (Table I) and fixed with 10% formalin. Spiral valves from these hosts were removed and examined for parasites in the laboratory.

Whole mounts of cestodes were stained with acetocarmine or Mayer's hematoxylin, dehydrated in ethanol, cleared in methyl salicylate, and mounted in Canada balsam. Serial transverse sections of specimens in paraffin were cut at 8- μ m intervals and stained with hematoxylin and eosin. Measurements were obtained using an Optimas image analysis system. Measurements include the range, followed by the mean, standard deviation, and sample size in parentheses. For measurements of 2 specimens, only the range is provided. All measurements are in μ m unless otherwise stated. Figures were drawn with the aid of a drawing tube. Specimens prepared for scanning electronic microscopy were post-fixed in 1% osmium tetroxide, infiltrated, and dried with Peldri II (Ted Pella Inc., Redding, California), mounted on stubs with contact adhesive tape, and sputter coated with gold. Type specimens and vouchers were deposited in the Coleção Helminológica do Instituto Oswaldo Cruz (CHIOC), Rio de Janeiro, Brazil; Instituto Nacional de Pesquisa da Amazônia (INPA), Manaus, Brazil; U.S. National Parasite Collection (USNPC), Beltsville, Maryland; Museo de Historia Natural La Salle (MHNLS), Caracas, Venezuela; and Harold W. Manter Laboratory (HWML), University of Nebraska, Lincoln, Nebraska.

DESCRIPTION

Anindobothrium n. gen.

Diagnosis: Phyllobothriidae. Scolex with 4 sessile or pedicellated quadrate, bilobed bothridia; each lacking longitudinal septa, bearing

transverse loculi and poorly differentiated apical suckers; marginal loculi present or absent. Genital pores marginal, in anterior $\frac{1}{4}$ of proglottid, irregularly alternating. Testes numerous. Vas deferens expanded to form distinct seminal vesicle joining cirrus sac more porally than aporally; internal seminal vesicle present or absent. Cirrus sac with armed cirrus. Ovary near posterior end of proglottid, X-shaped in cross section; arms symmetrical. Vagina anterior to cirrus sac; vaginal sphincter present. Vitelline follicles lateral. Uterus saccate, with poorly differentiated lateral diverticula or lacking diverticula. Parasites in spiral valve of sting-rays.

Taxonomic summary

Type species: *Anindobothrium anacolum* (Brooks, 1977) n. comb.

Etymology: The genus is named in honor of Dr. Anindo Choudhury.

Anindobothrium anacolum (Brooks, 1977) n. comb.

(Fig. 1A–C)

Synonym: *Caulobothrium anacolum* Brooks, 1977.

Diagnosis (modified from Brooks, 1977): Strobila acraspedote, apolytic, 6.8–15.4 mm long, composed of 13–32 proglottids. Scolex with 4 pedicellated, quadrate, bilobed bothridia bearing 22–23 transverse septa disjunct in center of bothridium forming 42–44 loculi; marginal loculi and longitudinal septum absent. Testes in anterior $\frac{3}{4}$ of proglottid, 34–45 in number. Vas deferens expanded to form distinct seminal vesicle joining cirrus sac more porally than aporally; internal seminal vesicle absent. Genital pore 19–29% of the proglottid length from anterior end, irregularly alternating. Vitelline ducts unequal in length, joining laterally at ovarian lobe.

Taxonomic summary

Host: *Himantura schmardae* (Werner) (Myliobatoidei: Potamotrygonidae).

Site: Spiral valve.

Locality: Caribbean Sea, 15 km, west of La Cienaga, Magdalena, Colombia (11°01'N, 074°15'W).

Holotype: USNPC 73969.

Paratypes: USNPC 73970, HWML 20265.

Anindobothrium lisae n. sp.

(Fig. 2A–D)

Description (based on 27 mature, 9 incomplete, and 5 immature specimens): Strobila acraspedote, apolytic. Mature worms 3.7–14.7 (8.94 \pm 3.2, 21) long, composed of 7–28 (16 \pm 5, 27) proglottids; immature worms 2.1–9 (3.8 \pm 2.9, 5) long, composed of 3–16 (10 \pm 6, 5) proglottids. Scolex 342–960 (529 \pm 165, n = 25) long by 573–1,218 (890 \pm 203, 26) wide in mature specimens, 344–793 (511 \pm 166, n = 6) long by 460–993 (748 \pm 213, 8) wide in immature worms, with 4 quadrate, bilobed bothridia. Bothridial pedicels ranging from inconspicuous up to 150–350 (254 \pm 66, 9) long according to maturity. Bothridia 377–923 (601 \pm 158, 13) long by 322–775 (595 \pm 156, 10) wide in mature worms, 399–816 (536 \pm 138, 7) long by 435–497 (475 \pm 28, 4) wide in immature worms, bearing 51–69 (61 \pm 7, 6) marginal loculi in mature worms, 55–57 (56 \pm 1, 6) in immature worms; transverse and longitudinal septa absent. Anterior sucker 45–80 (64 \pm 10, 14) in diameter in mature worms, 48–72 (62 \pm 9, 6) in immature worms. Immature proglottids 358–1,112 (775 \pm 238, 12) long by 282–504 (400 \pm 72, 12) wide; mature proglottids 631–2,348 (1,293 \pm 383, 84) long by 296–790 (456 \pm 90, 86) wide. Testes in anterior $\frac{3}{4}$ of proglottid, 32–118 (74 \pm 15, 165) long by 22–104 (52 \pm 19, 163) wide; 38–74 (54 \pm 8, 48) in number; 5–13 (8 \pm 2, 48) preporally, 10–26 (17 \pm 4, 48) postporally, 21–38 (29 \pm 4, 48) aporally. Vas deferens expanded to form distinct seminal vesicle joining cirrus sac more porally than aporally; internal seminal vesicle present. Cirrus sac in anterior $\frac{1}{4}$ of the proglottid, 103–319 (152 \pm 32, 67) long by 44–229 (86 \pm 28, 67) wide in mature specimens, contained spined eversible cirrus. Genital atrium inconspicuous. Genital pore 54–92% (74 \pm 6%, 70) of the proglottid length from posterior end, irregularly alternating. Vagina anterior to cirrus sac, vaginal sphincter inconspicuous, posterior portion expanded to form seminal receptacle. Ovary bilobed in frontal view, X-shaped in cross-section, follicular, poral lobes 132–482 (230 \pm 77, 66) long, apor-

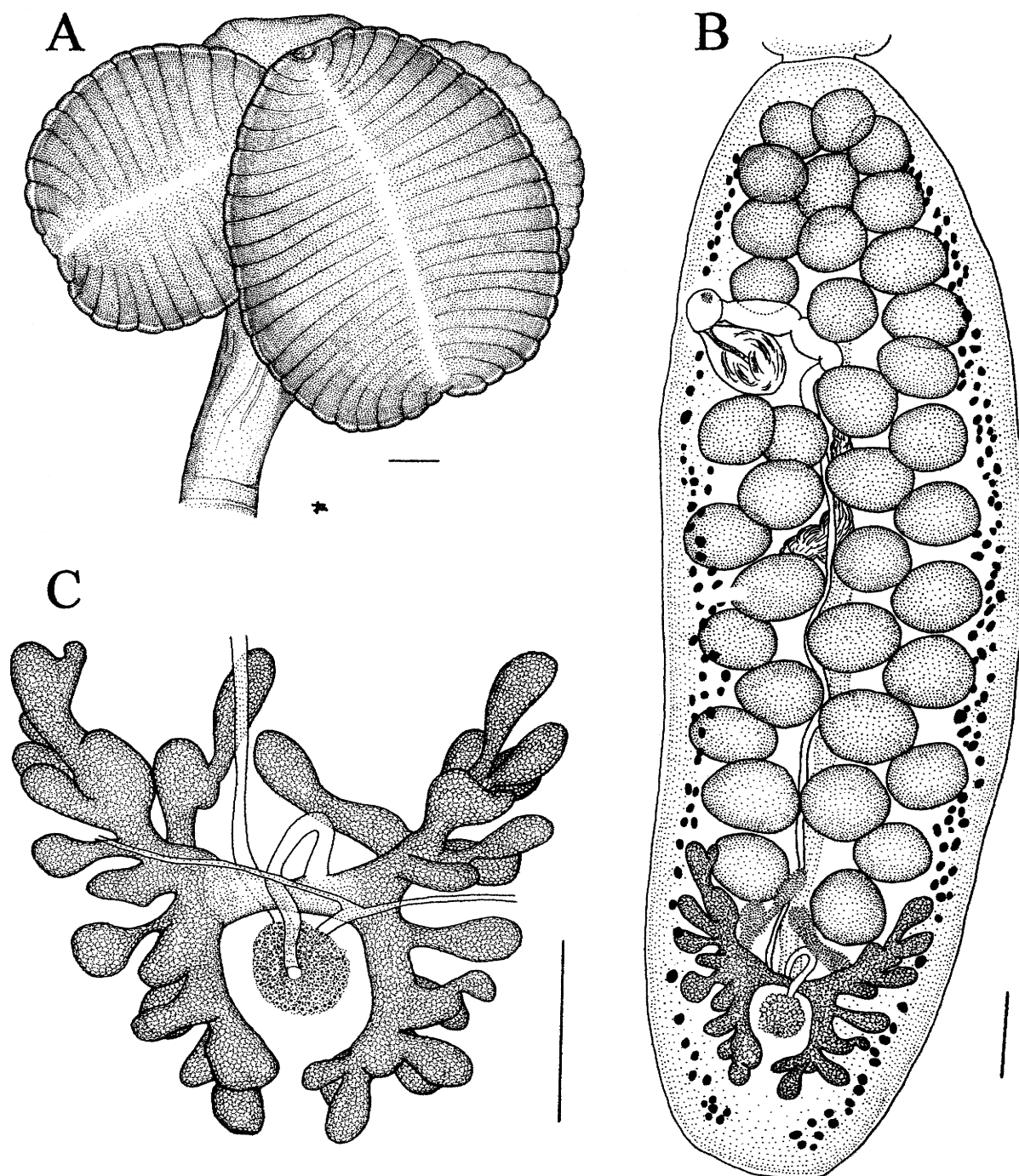


FIGURE 1. *Anindobothrium anacolum* n. comb. A. Scolex (USNPC 73969, holotype). B. Mature segment (USNPC 73970, paratype). C. Ovary (USNPC 73970, paratype). Scale bar = 100 μ m.

al lobes 117–453 (231 ± 78 , 66), Ovary 135–360 (233 ± 49 , 64) wide at isthmus in mature proglottids; anteroventral lobes converging anteriorly to midline of proglottid, but not fused. Vitelline follicles extending length of proglottid, 9–49 (27 ± 9 , 152) long by 8–35 (17 ± 5 , 152) wide. Vitelline ducts unequal in length, joining laterally at ovarian lobe.

Taxonomic summary

Host: *Potamotrygon orbignyi* (Castelnau) (Myliobatoidei: Potamo-
trygonidae).

Site: Spiral valve.

Locality: Rio Negro near Barcelos, Amazonas, Brazil (00°59'S,
062°58'W).

Holotype: CHIOC 34375.

Paratypes: INPA 0400ab, USNPC 91227-9, HWML 16379.

Etymology: This species is named for Lisa M. Nodwell.

Anindobothrium guariticus n. sp.

(Fig. 3A, B)

Description (based on 4 complete specimens): Strobila acraspedote, apolytic; mature worms ranging from 20 to 54 mm in length, composed of 68–126 proglottids. Scolex 550–611 long by 768–788 wide, with 4

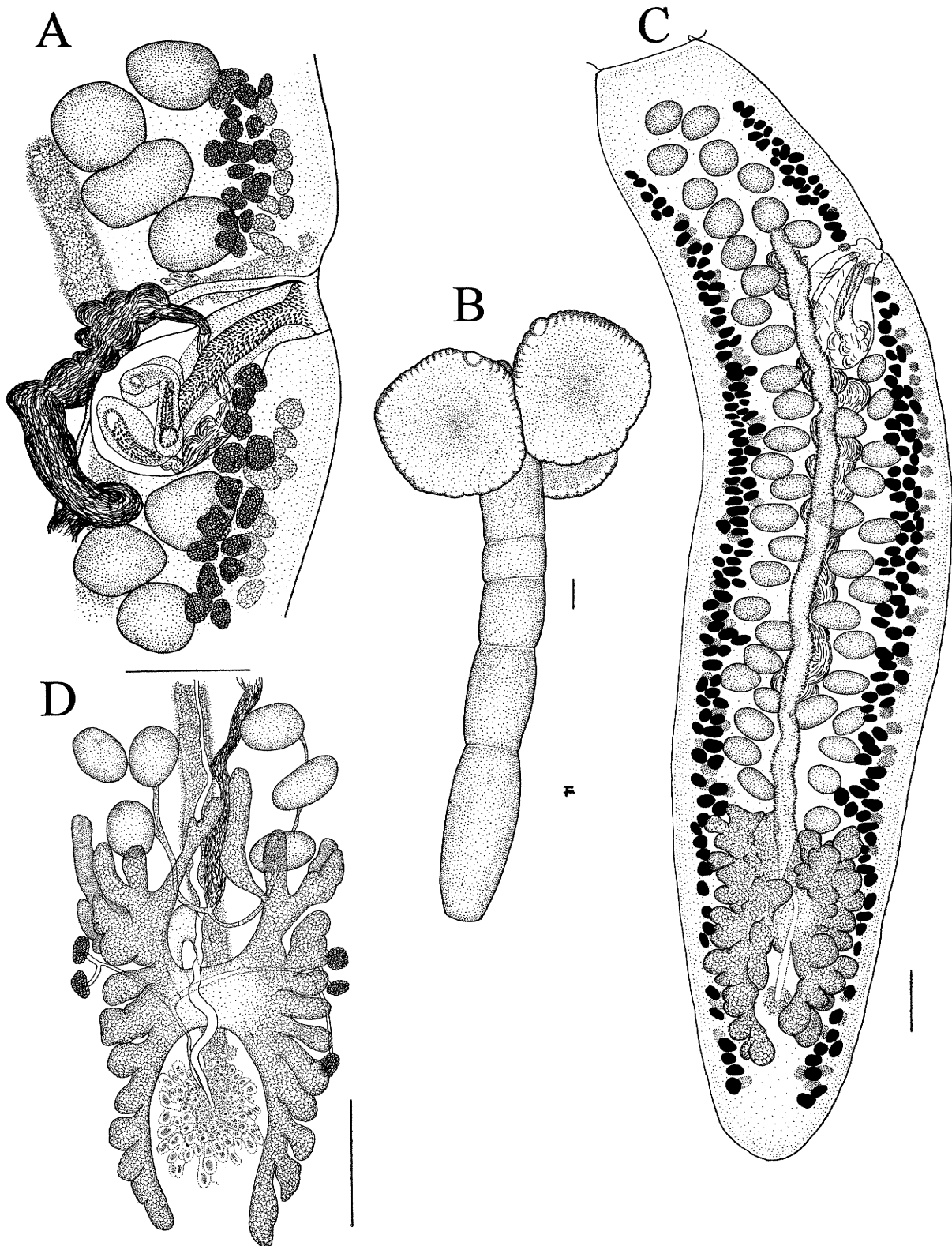


FIGURE 2. *Anindobothrium lisae* n. sp. **A.** Cirrus sac region. **B.** Immature specimen. **C.** Mature terminal segment. **D.** Ovary region. Scale bars = 100 μm.

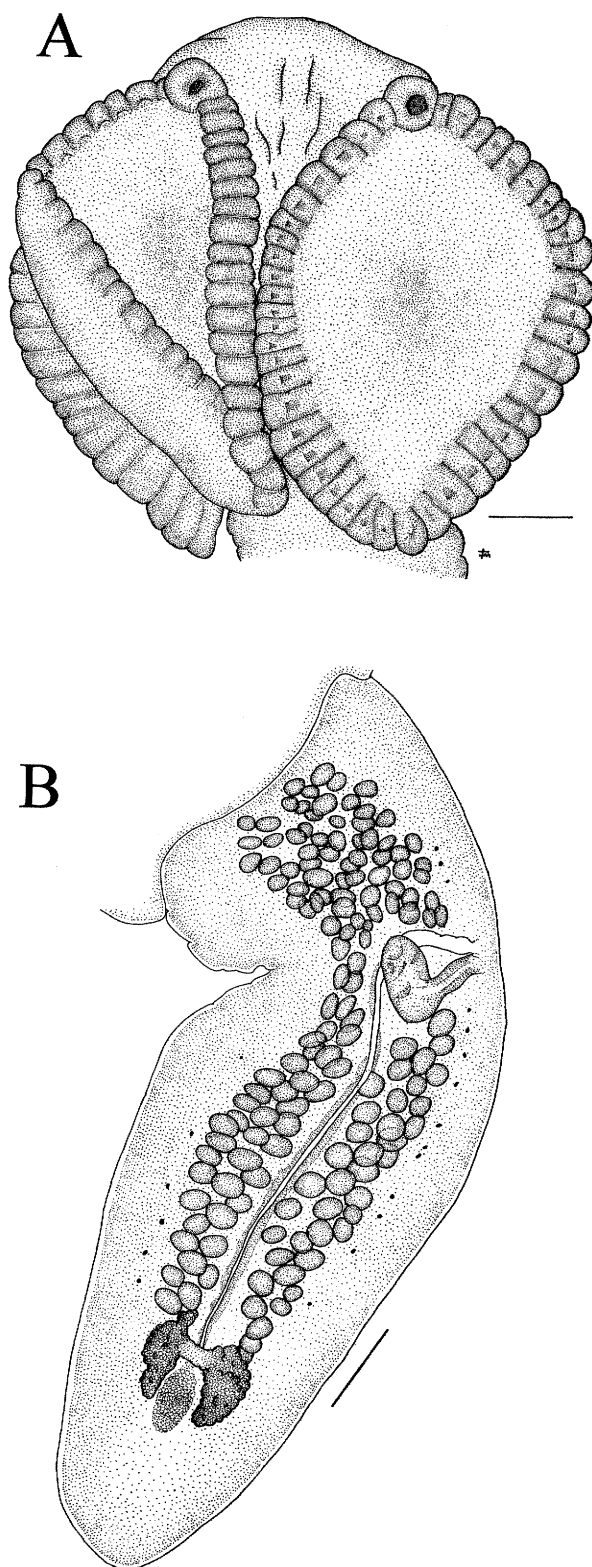


FIGURE 3. *Anindobothrium guariticus* n. sp. **A.** Scolex. **B.** Immature terminal segment. Scale bars = 100 µm.

quadrate, bilobed bothridia bearing approximately 46 marginal loculi; transverse and longitudinal septa absent. Anterior sucker 70–73 in diameter. Cephalic peduncle 2,250–4,500 long. Immature proglottids wider than long, mature proglottids up to 951 long by 341 wide. Testes in anterior $\frac{3}{4}$ of the segment, 24–79 (45 ± 17 , 15) long by 16–55 (31 ± 12 , 15) wide; 141–161 in number; 40–41 preporally, 38 postporally, 63–82 aporally. Vas deferens expanded to form distinct seminal vesicle joining cirrus sac more porally than aporally. Cirrus sac in anterior $\frac{1}{4}$ of the proglottid, 158–198 long by 47–127 wide, containing spined eversible cirrus. Genital atrium inconspicuous. Genital pore 75% of proglottid length from posterior end, irregularly alternating. Vagina anterior to cirrus sac, vaginal sphincter not observed, posterior portion expanded to form seminal receptacle. Ovary bilobed in frontal view, X-shaped in cross-section, follicular. Ovarian poral lobe 95 long, aporal lobe 92 long, 95 wide at isthmus in mature proglottids. Anteroventral lobes converging anteriorly but not fused. Vitelline follicles extending length of proglottid, 16–20 (17 ± 2 , 5) long by 8–16 (13 ± 3 , 5) wide.

Taxonomic summary

Host: *Paratrygon aiereiba* (Müller and Henle) (Myliobatoidei: Potamotrygonidae). Hosts deposited at MHNLS under accession numbers 6205 and 6206.

Site: Spiral valve.

Locality: Caño Guaritico, Hato El Frío, Orinoco Basin, Venezuela ($07^{\circ}52'N$, $069^{\circ}20'W$).

Holotype: MHNLS 6215.

Paratypes: USNPC 91230, MHNLS 6216.

Etymology: This species was named after its type locality, Caño Guaritico.

Remarks

Members of the new genus resemble species of *Pararhinebothroides*, *Rhinebothroides*, and *Anthocephalum* by having bothridia with poorly differentiated apical suckers and vasa deferentia expanded into external seminal vesicles. In particular, they further resemble members of *Pararhinebothroides* and *Rhinebothroides*, as well as *Anthocephalum cairae* Runhke, 1994 by having the vas deferens inserted near the poral rather than aporal end of the cirrus sac. However, distinctive differences in scolex morphology have traditionally been the basis for designating higher taxa among eucestodes and can be used to distinguish these groups. *Rhinebothroides* spp. possess marginal loculi, transverse septa, and a median longitudinal septum on each bothridium. *Pararhinebothroides*, as well as members of *Anthocephalum* and *Phyllobothrium kingae* Schmidt, 1978, possess marginal loculi that appears to be a basal synapomorphy for the entire group (Zamparo et al., 1999). *Anindobothrium anacolum* n. comb. possesses transverse septa and lacks marginal loculi, whereas *A. lisae* n. sp. and *A. guariticus* n. sp. possess marginal loculi and lack transverse septa.

Within *Anindobothrium* n. gen., the specimens of *A. guariticus* n. sp. available for this study were poorly preserved because they were collected from hosts that had been fixed prior to necropsy. Thus, some meristic characteristics of this new species should be interpreted with caution, e.g., strobilar and proglottid lengths, and should be re-evaluated after further collection of properly fixed specimens. Likewise, a more detailed description of ovary and cirrus sac is required. However, *A. guariticus* n. sp. is clearly a distinct and recognizable species. Compared to *A. lisae* n. sp., *A. guariticus* n. sp. is a robust cestode, differing from *A. lisae* n. sp. by having greater number of proglottids (68–126 vs. 7–28) and number of testes (141–161 vs. 38–74). In this regard, *A. anacolum* more closely resembles *A. lisae*.

DISCUSSION

The taxonomy of phyllobothriids has long puzzled parasitologists (see Runhke, 1994), because many of the higher taxonomic groups are not defined on the basis of unique characters, but instead are based on a combination of nonunique features. Also, because phyllobothriids show great morphological diversity and are relatively poorly known, many higher level taxonomic diagnoses have been emended to accommodate new taxa

to the point that these diagnoses could be applied to many taxonomic entities. A classic example is *Phyllobothrium* van Beneden, 1849. From its original conception by van Beneden (1849), to workers who proposed much broader concepts of *Phyllobothrium* (e.g., Southwell, 1925; Yamaguti, 1959; Schmidt, 1986; Euzet, 1994), the generic diagnosis became so generalized that it could be applied to virtually all nonhooked, bothridium-bearing tetraphyllideans (Runhke, 1996).

Consistent application of a single systematic principle will improve the taxonomy of phyllobothriids. All higher taxa proposed should be diagnosed by at least 1 apomorphic trait, the quality of which should be highly general. This is especially true when one is proposing a monotypic higher taxon, because we expect higher taxa to include more than 1 species. In the present study, simply designating apomorphic traits for new species could have permitted us to designate 2 genera, 1 monotypic (for *A. anacolum*) and 1 comprising 2 species (for *A. lisae* and *A. guariticus*).

Diagnosis based on apomorphies will always produce more stable taxonomic structures than those based on overall similarity that may include plesiomorphies and homoplasies. An example within phyllobothriids is the resurrection of *Anthocephalum* Linton, 1890 by Runhke (1994). The genus had been considered to be a junior synonym of *Phyllobothrium*, but Runhke (1994) considered *Anthocephalum* a coherent phenetic group and resurrected the genus. Zamparo et al. (1999), however, found that this coherent phenetic group was paraphyletic if *Pararhinebothroides* and *Rhinebothroides* were excluded from it. By contrast, the 3 species assigned to *Anindobothrium* n. gen. form an apparent monophyletic group, based on their shared possession of 3 putative synapomorphies: (1) genital pores in the anterior ¼ of the proglottid, a trait that is unusual but not unique among phyllobothriids; (2) anteroventral ovarian lobes converging to the center of the proglottid, a character not previously reported for phyllobothriids; and (3) ovarian lobes comprising a loose network of digitiform processes.

Finally, if those tetraphyllideans possessing external seminal vesicles inserted into the cirrus sac orally represent a clade, the present study suggests that a new phylogenetic assessment of the position of *P. hobergi* and *A. cairae* within the larger group may be necessary. *Anthocephalum alicae* Runhke, 1994, *A. cairae*, *Anthocephalum centrurum* (Southwell, 1925), and *P. hobergi* exhibit ovarian lobes that expand laterally to such an extent in mature proglottids that the vitelline follicles are interrupted at the ovarian level. This trait is not found in basal members of *Anthocephalum*, in *Anindobothrium* spp., or in *Rhinebothroides* spp. (see Runhke, 1994; Zamparo et al., 1999). In the analysis by Zamparo et al. (1999), the vitelline distribution exhibited by *Rhinebothroides* spp. was considered to be a consequence of the modification of the ovarian shape in *Rhinebothroides*, producing a reversal in vitelline structure. It is possible, however, that the condition exhibited by *P. hobergi* and some members of *Anthocephalum* is a synapomorphy for those species. If so, the anterior insertion of the external seminal vesicle in *A. cairae*, *Pararhinebothroides*, *Rhinebothroides*, and *Anindobothrium* may be homoplasious.

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